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ADAPTATIONAL PROBLEMS INVOLVED IN THE HISTORY OF THE GLACIAL RELICTS OF EURASIA AND NORTH AMERICA *

BY

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The communication is concerned with the so-called glacial relicts found in fresh waters of Eurasia and North America, and more particularly with those having marine relatives. The history of these animals, crustaceans and fishes, has included a primary adaptation (seemingly in a Siberian ice-dammed lake of the penultimate glaciation) to fresh water, with retained capacity to tolerate dilute sea water, the environment which evidently offers optimal conditions for the species concerned. In the case of Northern Europe, the relicts in the course of their immigration during the last glaciation have undergone repeated adaptations to fresh and again to brackish water. The nature of these adaptations is discussed.

As is well known, many lakes of North Europe harbour a peculiar faunal element which was introduced into the area during the Glacial Epoch of the Pleistocene. Most of these animals, the so-called glacial relicts, are identical with or closely related to forms living in the Arctic Sea.

The glacial relicts of North European lakes include the following fish and crustacean species:

Mysidacea: *Mysis relicta* Lovén

Isopoda: *Mesidotea entomon* (L.)

Amphipoda: *Gammaracanthus lacustris* G. O. Sars

Pontoporeia affinis Lindström

Pisces: *Myoxocephalus* (*Cottus*) *quadricornis* (L.)

The above list is confined to the relicts with marine relatives, because these are the forms that I am going to discuss on this occasion. Other well-known glacial relicts include the amphipod *Pallasea quadrispinosa* and the copepod *Limnocalanus macrurus-grimaldii*.

* Work presented at the First Session of Animal Physiology (Cluj, May, 25—28, 1965).

The presence of remnants of a glacial marine fauna in lakes of Northern Europe was first reported from some lakes in Sweden, more than a hundred years ago. Subsequent research has showed that the same animals also occur in many other North European lakes, and most of them also in the Baltic Sea. Furthermore, several of the species concerned have proved to live in the Caspian Sea, in fresh waters of northern Asia and in lakes of North America and adjacent arctic islands.

The immigration of the glacial relicts into their present sites presents a fascinating zoogeographical problem. On this occasion I hope to be able to show that the invasion history of these animals also involves physiological and ecological problems of considerable interest. The prevailing views of today concerning this history may be summed up as follows (Segerstråle 1957, 1962).

The glacial relicts of marine origin came into existence in a large ice-lake that was formed in western Siberia during the penultimate glaciation, more than a hundred thousand years ago. The lake resulted from the damming-up effect of glaciers coming from the coast of Siberia and progressing southwards. Together with coastal waters which were sluiced up, as it were, in front of the advancing ice-cap, marine animals became isolated in the ice-dammed lake. As a consequence of the dilution of its water, most members of the trapped marine fauna perished, but some of them — the ancestors of the relicts of our days —, succeeded in adapting themselves to the new environment, which finally became totally fresh. Parallel with the physiological adaptation, the animals concerned also underwent morphological modifications. These evolutionary processes resulted in the species known as marine glacial relicts. Apart from their relict occurrence, the range of these animals comprises the coastal waters of northern Russia, northern Asia and North America. The sea was reached from the Siberian ice-lake when this disappeared in connection with the melting of the damming glaciers. *Mesidotea entomon* seems to have evolved from the closely related marine *M. sibirica* (Gurjanova 1946), *Pontoporeia affinis* from *P. femorata* (Lomakina 1952), *Gammaracanthus lacustris* from *G. loricatus* (Lomakina l. c., Segerstråle 1957) (in arctic waters today the latter is represented by the intermediate brackish-water *G. loricatus* subsp. *aestuariorum* and *G. l.* var. *ostiorum*; Lomakina 1952, Johnson 1962) and so on (see Fig. 1).

In connection with the physiological adaptation to fresh water in the ice-lake, the surviving remnant of the coastal marine fauna apparently lost their ability to tolerate sea water of normal salinity. This is indicated by the fact that all the animals concerned are today, in marine situations, confined to brackish water. On the other hand, such diluted marine areas are clearly preferred in comparison to fresh waters. Evidence of this is the larger size that the relict species reach in brackish situations; in many cases they also exhibit a fuller morphological development there (cf. Segerstråle 1962). An especially illustrative example of this point is offered by *Myoxocephalus quadricornis*. If we compare specimens of this fish from brackish regions, — say, the Baltic —, with others from neighbouring lakes, it is found that the latter are much smaller and that the four

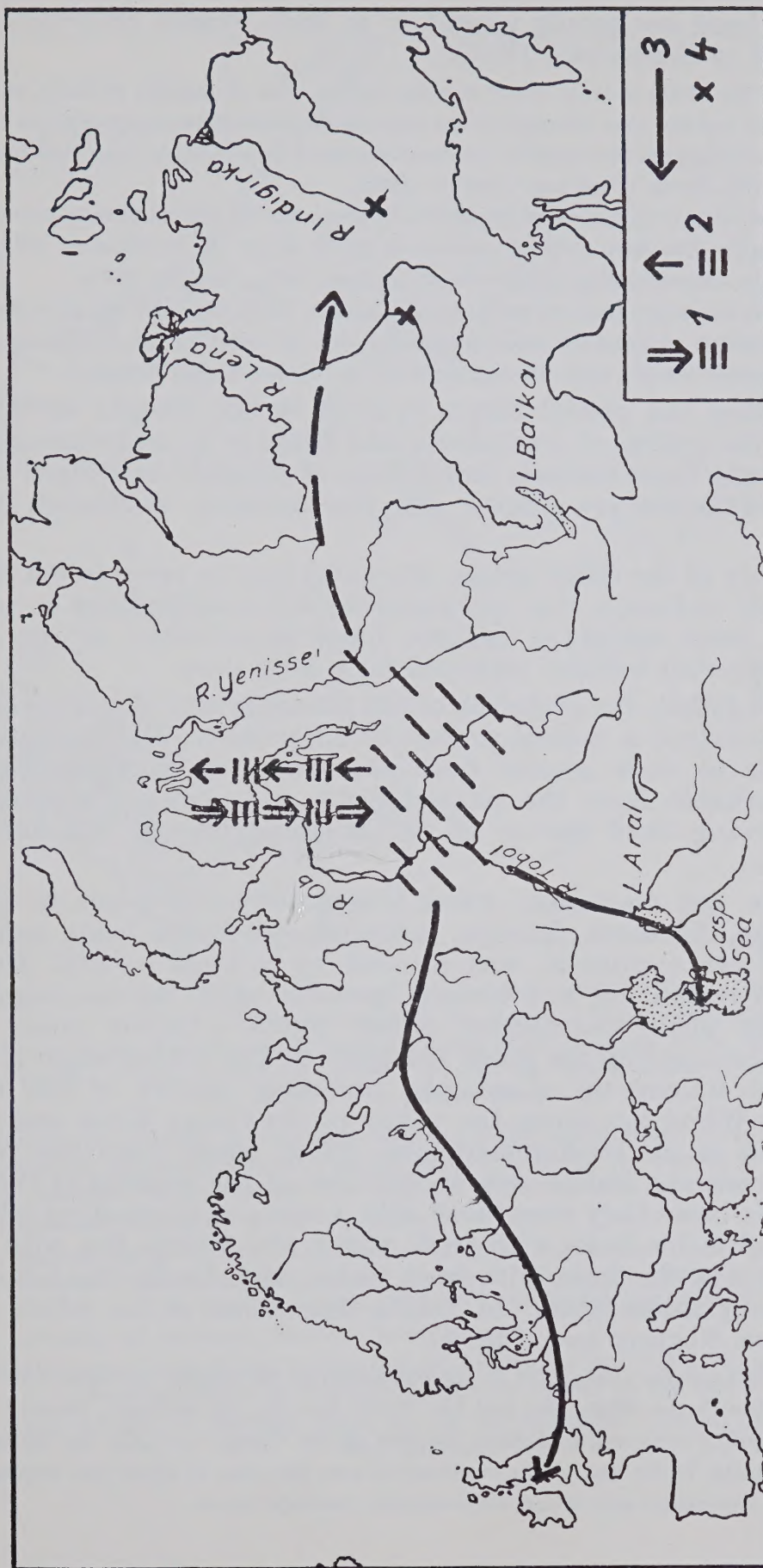


Fig. 1. — The suggested role of the Siberian ice-lake of the maximum (= Riss) glaciation in the development and spread of glacial relicts of marine origin. The extent of the lake at its highest level tentatively hatched.

- 1) Marine animals are sluiced up from the sea in front of the advancing ice, and, in some cases, having lost their ability to tolerate water of full salinity, and, in some cases, having undergone morphological modification.
- 2) Following the melting ice-margin, they return to the sea, having lost their ability to tolerate water of full salinity, and, in some cases, having undergone morphological modification.
- 3) Migration of these, originally marine, forms into Europe and the Caspian Sea, and to the east.
- 4) Inland localities of *Mesidotea entomon* in eastern Siberia.

(After Segerstråle 1957)

“horns” on the head are totally absent or at least weakly developed (see Figs. 7 a and 7 b in Segerstråle 1957).

Other cases of the effect of fresh water in reducing the size of aquatic animals, at home in brackish water, are known. One example is the amphipod *Pontogammarus maeoticus* (Sow.) Mart. : the main form living off the coast of the brackish Black Sea is larger than that found in lakes isolated from this basin (Pora and Căraușu 1938).

An idea of the salinity tolerance of the relicts is given by the following data concerning the Baltic. In this basin *Mesidotea entomon* penetrates up to about the isosaline of 15‰, for *Pontoporeia affinis* the corresponding salinity limit is about 18‰ (Mulicki 1957).

In the previous literature (see, for instance, Zenkevich 1959) the view has also been advanced that the evolution of brackish-water animals is due to isolation of marine ancestors in gradually diluted saline basins, with ensuing inability to tolerate higher salinities.

The fact that the glacial relicts evolved in the ice-lake of Siberia are confined to the groups of crustaceans and fishes is by no means surprising, since amongst these animals many cases of a highly developed capacity for osmoregulation are known (cf., for instance, Zenkevich 1957, Kinne 1964 b).

The inability of the relict species discussed here to tolerate sea water of normal salinity indicates that the physiological modifications to which their ancestors were subjected became fixed genetically; so we may infer that the Siberian ice-lake persisted for a long time.

As we have found, the evolution of the glacial relicts of marine origin seems to have involved a radical process of adaptation. The immigration of these animals to their present fresh-water sites in Northern Europe is no less remarkable from the physiologist's and ecologist's points of view. The following brief survey of the invasion history will provide evidence of this.

During the last glaciation, which is assumed to have set in about 70,000 years ago, Northern Europe, including the Baltic basin and adjacent parts of the continent, was covered by a large ice-cap. Hence, invasion of the region did not become possible until the ice began to melt away. This phase commenced about 15,000 — 20,000 years ago. Details of the immigration are given in figure 2. The initial stage of this process was the sluicing-up of animals, including species of the relict group, from the White Sea along the valley of the Onega River and their ensuing isolation in an ice-dammed lake. From these lakes the relicts were able to invade the Baltic area at the time of the melting of the ice-cap. In the Baltic basin they were faced with a series of alternating salinity regimes : the Baltic Ice Lake with fresh water, the Yoldia Sea with brackish water, the Ancylus Lake with fresh water, and, finally the Littorina Sea with markedly saline water. In Yoldia times some of the relicts even reached southern Norway (see Fig. 2).

Some geologists assume that, prior to the formation of the Baltic Ice Lake, the Baltic basin was connected with the White Sea and the North Sea (cf., for instance, Donner 1965). However, this possibility does not annihilate the role of the Onega Ice Lake for the spread of relict species from the White Sea to the continental area nor does it affect the sequence of their adaptations to non-saline and saline environments outlined below.

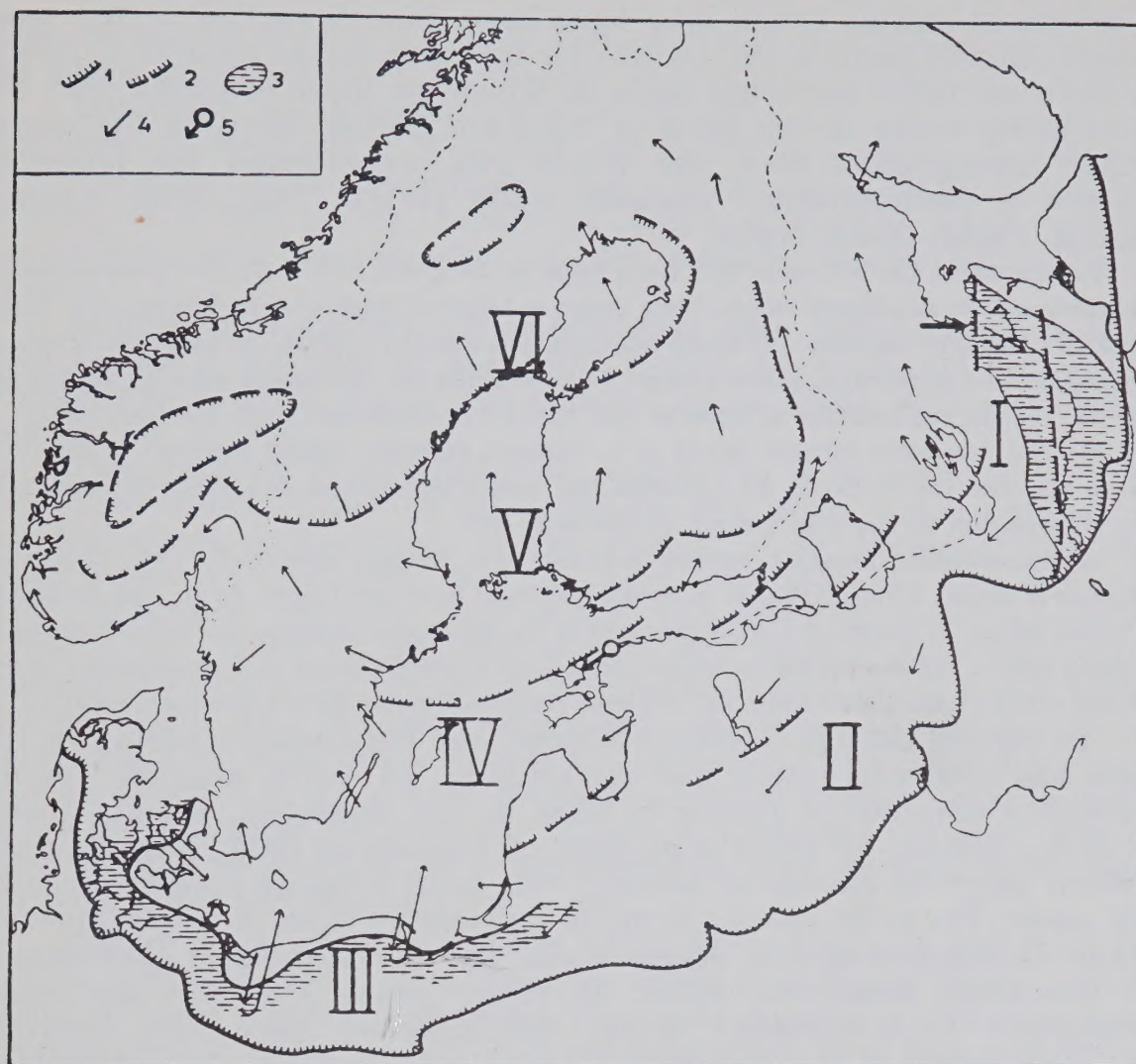


Fig. 2. — Survey of the immigration of the relicts, dealt with in Fig. 1, into Northern Europe in connection with the last (= Würm) glaciation.

1) Maximum extent of the ice-cap. 2) Tentative positions of the ice-margin during the melting phase. 3) Onega ice-lake. 4) Spread of relicts to northern Germany and adjacent areas. 5) Arrival of other relicts in the open Baltic.

I) Sluicing up of water and animals from the White Sea, in front of the advancing ice-cap; formation of the Onega ice-lake; spread westwards during the waning phase of the ice-cap, along dammed waters; spread northwards, up to the Kola Peninsula, from I. Onega.

II) Continued westward spread of relicts.

III) Sluicing up of relicts, with Baltic water, to continental areas in connection with an advance of the ice-cap; subsequent return of relicts to the Baltic as the ice-margin retreated again. Stage of the Baltic Ice Lake.

IV) Invasion of southern Sweden. Same stage.

V) Spread over Finland and across central Sweden, in late Yoldia times, to southern and southwesternmost Norway; northward spread in the Baltic basin.

VI) Final spread, in. Ancylus times, to the northernmost part of the Gulf of Bothnia and adjacent areas.

(After Segerstråle 1957)

During the saline phases of the Yoldia Sea and the Littorina Sea the relicts of marine origin may have been able to survive in the most strongly diluted parts of the Baltic; for instance, in the mouths of rivers. But even so, there are some cases in which we must conclude that the relicts living today in the lakes of Northern Europe have, in the course of their immigration from the White Sea, experienced the following sequence of environments: brackish water (White Sea)—fresh water—brackish water—fresh water.

For instance, the following two cases seem to be quite clear: (1) The populations of *Pontoporeia affinis* and *Mysis relicta* living today in lakes of southwestern Norway (cf. Segerstråle 1957). Route of invasion: (a) White Sea (brackish water), (b) Baltic Ice Lake (fresh water), (c) migration to SW Norway, across central Sweden, along the Norwegian coast in diluted sea water (cf. Fig. 2), (d) isolation in lakes of SW Norway in connection with the land uplift.

(2) The *Mesidotea entomon* found in L. Mälaren (eastern central Sweden). — Route of invasion: (a) and (b) as above, (c) Littorina Sea (brackish water of comparatively high salinity), (d) isolation in the lake formed as the land rose.

Gammaracanthus lacustris deserves a special note, being a case on its own. This relict crustacean is absent from the Baltic of today but must have lived there up to and including the Yoldia phase, as indicated by the presence of the species in southern Norway. It has been concluded that it perished in Baltic waters during the Littorina phase as a consequence of the combined effect of too high salinity and too high temperature (for details, see Segerstråle 1957).

In regions outside Northern Europe, the immigration history of the relicts has apparently been less complicated. In North America, for instance, the presence of relicts in lakes of the continent, which, is also due to the sluicing-up effect of glaciers (cf. Segerstråle 1962), has, after all, involved only one change of salinity, viz. from brackish coastal areas to fresh water. The relict species living in continental lakes of North America include *Pontoporeia affinis*, *Mysis relicta*, and *Myoxocephalus quadricornis* (*M. thompsoni*, McAllister 1959). In recent years *Mesidotea* and *Gammaracanthus* (as *G. loricatus* subsp. *aestuariorum*) have been recorded from lakes situated in some of the Arctic islands north of the American continent (Johnson 1962, 1964) and it is suggested that these populations were isolated from the surrounding sea in connection with the land upheaval. Hence, in this case too, only one change of environment would have occurred.

The fact that in Northern Europe populations of glacial relicts have repeatedly survived the shift from fresh to brackish water, and vice versa, poses the question whether these adaptations have been due to selective processes or to a wide phenotypical tolerance range in the animals concerned. Before discussing this problem, certain physiological studies should first be reviewed.

Experiments with *Mesidotea entomon* have been performed by Bogucki (1932), Belyaev (1949 a; cf. Belyaev 1957), and Lockwood & Croghan (1957). This work showed that specimens of the isopod taken from the brackish Baltic survived at most for some days if transferred to fresh or very strongly diluted saline water (Belyaev: less than 3‰). By contrast, Baltic specimens proved to tolerate, without difficulty, salinities of up to 40‰ (Belyaev), and the same result was even obtained

when *Mesidotea* from a Swedish lake (Vättern) was placed directly in sea water of full salinity (Plymouth water) (Lockwood and Croghan).

Lockwood and Croghan found a markedly high haemolymph concentration in fresh-water *Mesidotea* and regard this feature as primitive (i. e., connected with the comparatively recent marine origin of the crustacean; as is well known, lacustrine species of ancient origin typically have a low blood concentration; cf., for instance Beadle 1957, Lockwood 1962).

Belyaev also carried out experiments with *Mysis relicta* (Belyaev 1949 b). As in the case of *Mesidotea*, Baltic specimens did not tolerate transference to fresh water, but endured saline water with considerable salinity, up to 30‰.

These results of physiological studies are in accordance with the conclusion drawn earlier on this occasion, that fresh water represents a less favourable environment to the glacial relicts discussed than does saline water. At first sight, they also seem to support the idea of a genotypic difference between fresh-water and brackish-water populations of the relicts. However, one has to take into consideration the extreme slowness of the dilution process in the course of their immigration history in comparison with ordinary laboratory conditions. Of interest in this connection are the results obtained by Karpevich (1940), who found that Caspian bivalves of the genera *Monodacna* and *Dreissena* can be adjusted to life in pure fresh water if the salinity is gradually lowered. (For the importance of acclimatization in experimental work see also, for instance, Schlieper 1960 and Kinne 1964 a, b).

In fact, there are some features which seem to suggest that the relicts may be endowed with a wide tolerance range with regard to the salinity regime of their environment. What I have in mind is, on the one hand, the shortness of the time allotted to the glacial relicts of Northern Europe for a repeated evolution of fresh-water and brackish-water races — in some cases less than 6,000 years for the shifts fresh water — brackish water — fresh water —, and, on the other hand, the distribution pattern of certain other aquatic animals. In the Sea of Azov and the Caspian Sea, relicts of the Sarmatic Sea (again mostly crustaceans and fishes) are found not only in brackish situations but also far up the neighbouring rivers (Ekman 1953, Caspers 1957, Zenkevich 1959). This is seemingly the sequel of an earlier phase when the basins concerned covered a wider area and were strongly diluted. Cf. also Kinne (1964 b, p. 151): “Nach Emery et al. (1957) ist . . . gerade die Euryplastizität der ästuarinen Organismen ein genetisches Merkmal, welches offenbar nur schwer zu erwerben ist, das aber — einmal vorhanden — im Sinne der Evolution sehr konservativ ist”.

At present, no final explanation can be offered for the repeated adaptations in opposite directions which have occurred within populations of the glacial relicts. At any rate, the feature as such is remarkable. It is for this reason that I have drawn attention to it before this audience. As all of us know, the combined efforts of physiologists and ecologists are today focussed on the problems of adaptation.

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POSTSCRIPT (1967). At the time of writing this article, the present author was not aware of Kozhov's comments on the supposed ice-lake in western Siberia (Kozhov 1963).¹

The existence of such an ice-lake had been concluded by Pirozhnikov on the basis of biological evidence and results obtained by Russian geologists (for instance, signs of a spillway at the head of R. Tobol; cf. Segerstråle 1957, p. 94). According to Kozhov (p. 225), modern investigations in the West-Siberian Lowland reveal no trace of an extensive ice-dammed basin, neither are there any indications of an ancient run-off from it towards the Caspian Sea. However, Kozhov admits that dammed glacial lakes, even very big ones, may have existed in North Siberia in Glacial times. Considering this, the present author is disinclined to abandon the essence of his view that Siberian ice-dammed waters played a role in the prehistory of the glacial relicts. On the contrary, he anticipates that future geological research will provide evidence of the existence, somewhere in Siberia at the time of the penultimate glaciation, of proglacial waters where the relict species evolved and from which they were able to spread along the margin of the ice-caps and, through overflow, southwards. Otherwise, the existence, on the one hand, of relicts, including some freshwater fishes of eastern origin, in lakes of the British Isles and, on the other, of a relict crustacean such as *Pallasea* in the North European region and in the Caspian Sea, seem inexplicable (cf. Segerstråle l.c.; Ekman 1959).²

¹) M. Kozhov: Lake Baikal and its life. Junk Publishers, The Hague. 1963.
²) S. Ekman: En översikt av de marin-glaciala relikternas historia med ledning av S. G. Segerstråles senaste arbeten [A survey of the history of the marine-glacial relicts on the basis of the latest papers of S. G. S.]. Ymer 1959: 1, 68—74. Stockholm.

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